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Original research article

## Harvesting, census timing and “hidden” hydra effects

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## ABSTRACT

Population control in some form of harvesting might be expected to reduce population size, but quite the opposite can happen due to the hydra effect. This phenomenon describes an increase in population size with increased mortality. One mechanism causing hydra effects is the temporal separation of (i) harvesting and (ii) density-dependent reproduction. Here we consider discrete-time models of these two processes. It is commonly believed that harvesting needs to precede reproduction for a hydra effect to occur. We show that, by contrast, hydra effects also take place for harvest after reproduction. Due to the timing of population census, however, the hydra effect will not be measured and thus remains ‘hidden’. As a consequence, managers may miss out on the opportunity to increase both the yield and the remaining stock of renewable resources. If harvesting aims at controlling pest species, management interventions may backfire in the sense that the pest increases rather than decreases—and, to make things even worse, this may actually go unnoticed. To remedy these undesirable consequences, we propose a modelling framework that can reveal hidden hydra effects. Our results are based on rigorous mathematical proofs that the order of two events does not matter for standard harvesting/hunting strategies.

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## 1. Introduction

Harvesting constitutes a key element in the management of populations and renewable resources such as fishery or forestry. Various forms of harvesting (e.g., hunting, culling, trapping, pesticides) are used to exploit populations for economic benefit and to control species that are considered pests or nuisances. In recent years, it has been increasingly recognised that harvesting can have a rather unexpected outcome, namely the so-called hydra effect (Abrams, 2009). This describes the seemingly paradoxical increase in population size when the population’s mortality is increased. Different mechanisms can lead to a hydra effect. The one considered here is based on harvesting a population with discrete-time structure and overcompensatory density dependence (mechanism 2 in Abrams, 2009). As harvesting reduces population size, it releases the population from competitive pressure and thus prevents population crashes typical of scramble competition. Hence, this may lead to an increased population density. A list of references with empirical evidence for these hydra effects can be found in Zipkin et al. (2009).

There are myriad of models considering the two processes of harvesting and density-dependent reproduction. Some of them

assume harvesting preceding reproduction (e.g., Zipkin et al., 2009; Yakubu et al., 2011; Liz and Ruiz-Herrera, 2012), whereas others assume it following reproduction (e.g., Sinha and Parthasarathy, 1996; Vandermeer and Yodzis, 1999; Schreiber, 2001; Liz, 2010b). There is a prevailing view in the literature that the kind of hydra effect described above (i.e., due to overcompensation) can only occur if harvesting takes place *before* reproduction, but not if harvesting takes place afterwards. For instance, in his seminal review Abrams (2009, p. 469) concludes: “What is essential for a hydra effect is that mortality precedes or is concentrated in the early part of a strongly density-dependent stage”. According to this common belief (see also Seno, 2008; Kokko, 2001), there cannot be a hydra effect if harvesting takes place *after* reproduction—a belief we will show not to be always true.

If we consider the simple case of only two processes like harvesting and reproduction, their relative temporal order is actually the same (Åström et al., 1996). For the sake of illustration, let  $H$  and  $R$  denote the processes of harvesting and reproduction, respectively. Now consider the two compositions of harvesting taking place before and after reproduction, which after three iterations each give the respective sequences

$$H R H R H R \dots \text{ and } R H R H R H \dots$$

Obviously, the only difference between these two compositions is the time of measurement of population size after what we define to

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be one cycle (iteration). Hence, we may expect that the stability properties of the two compositions are the same, as are the population sizes after each specific process (Åström et al., 1996).

From a mathematical perspective, however, this argument is not clear-cut. For certain processes different census timing may lead to different global behaviour in the population dynamics (we give an illustrative example in Section 3). In this paper, we provide rigorous results that the standard harvesting strategies do not show such 'global differences'. Hence, the order of events does not matter for the harvesting strategies considered.

It is noteworthy that we understand 'harvesting' in a broad sense, i.e., as any action removing a part of the population. Hence, our results can also be interpreted from the point of view of pest control through pesticides, for example. Moreover, our conclusions are not limited to harvesting and reproduction specifically, but also apply to other processes. For instance, the importance of census timing has been studied and highlighted by Lutscher and Petrovskii (2008) in the context of spatial dispersal.

One of our main results is that hydra effects can also occur for harvesting following reproduction. Consequently, hydra effects can be much more prevalent than previously thought. They just go unnoticed due to the particular choice of census timing. In order to remedy such "hidden" hydra effects, we propose a mathematical framework that helps revealing them. In the discussion, we argue that hydra effects that are overlooked may lead to wrong population estimates and misguide management recommendations.

## 2. Temporally structured processes

When population dynamics are measured in discrete time, they can be described by difference equations of the form

$$x_{n+1} = f(x_n),$$

where  $x_n$  denotes the population size at the  $n$ th time step and function  $f$  the population production in one such time step. It is customary to choose a time step that has biological meaning, e.g., corresponding to generation length. Typically, there is not just only one process like reproduction taking place within one time step. Instead, there may be multiple processes like birth, death, migration, predation, harvesting, etc., some of which can be combined to give well-known production maps (Ricker, 1954; Beverton and Holt, 1957; Eskola and Geritz, 2007). If these processes do not take place simultaneously but sequentially, we get a composition of the form

$$x_{n+1} = f_p \circ f_{p-1} \circ \dots \circ f_1(x_n) = (f_p \circ f_{p-1} \circ \dots \circ f_1)(x_n),$$

where the functions  $f_i, i = 1, \dots, p$ , describe the individual processes. The relative order of the processes  $f_i$  thus introduces a temporal structure within a single time step, with process  $f_1$  preceding  $f_2$  and so on.

In general, there are  $p!$  different ways to arrange a sequence of  $p$  processes. However, their relative order differs in  $(p - 1)!$  cases only. In the remaining sequences, the relative positions are the same. Åström et al. (1996) have argued that models of processes in the same relative order (or if all processes are density-independent) share the same stability properties. Moreover, population sizes after each specific process are the same (but population sizes differ when measured only after a complete cycle because then the census takes place after different processes and misses out on the complementing ones in between).

In the following, consider the two processes of reproduction, described by a production function  $f$ , and harvesting, described by a function  $h$  giving the population size that survives harvesting.

There are two possible ways to arrange them in a sequence:

$$x_{n+1} = f(h(x_n)), \tag{2.1}$$

$$x_{n+1} = h(f(x_n)), \tag{2.2}$$

where the former one can be interpreted as harvesting before reproduction and the latter one as harvesting after reproduction. As pointed out before, however, in iterations of both models the relative order of the two processes stays the same, as each iteration is simply a sequence of '... reproduction, harvesting, reproduction, harvesting...' and so on. That is, each harvesting process follows as well as precedes a reproduction process. The difference between model (2.1) and (2.2) is just when we census the population, namely either after reproduction or harvesting, respectively. It therefore seems more appropriate to talk about the timing of population census rather than the timing of harvesting.

Furthermore, following the argument by Åström et al. (1996), we may expect that there is no qualitative difference between the two models and, if population sizes were censused after each individual process, no quantitative difference either. In the next section, however, we redraw an example from the literature illustrating that this is not always the case. This constitutes an unsatisfying situation, because we cannot be sure that the dynamics of the two models are equivalent.

For example, if  $f$  is one of the usual overcompensatory population maps like the scaled Ricker model, i.e.

$$f(x) = x e^{r(1-x)}, \quad r > 0, \tag{2.3}$$

and  $h$  describes the population surviving constant effort harvesting, where we remove a constant fraction  $\delta$  of the population, i.e.

$$h(x) = x(1 - \delta), \quad \delta > 0, \tag{2.4}$$

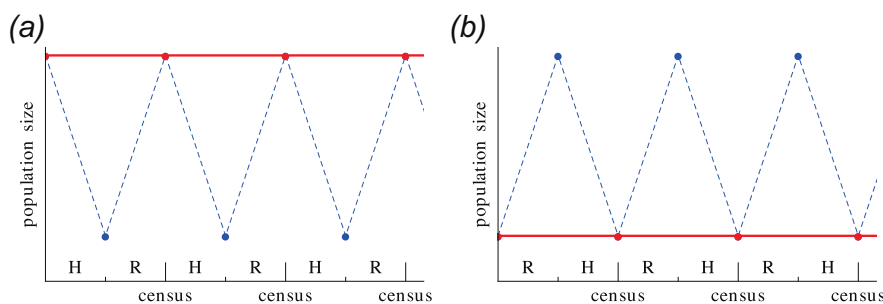
then it is well-known that model (2.1) of 'taking the census after reproduction' can exhibit the hydra effect. The arising question is whether or not model (2.2) of 'taking the census after harvesting' exhibits the same dynamics, including the hydra effect.

In this paper, we will provide proof that hydra effects indeed occur in both models, but that we cannot always measure them due to the choice of census timing. This is illustrated in Fig. 1. To be a bit more precise, this situation holds for general overcompensatory population dynamics (for which the Ricker model is an example) and the following three harvesting strategies: (i) constant effort harvesting, also called proportional harvesting or proportional feedback (PF); (ii) constant yield harvesting, also called constant feedback control (CF); and (iii) threshold harvesting, also called limiter control (LC). In the next section, however, we consider an example with target-oriented control leading to a different result.

## 3. When the order of two events matters—an example

According to the arguments of Åström et al. (1996), the order of events does not matter if their relative order is the same. To show why this statement has to be interpreted with some caution, we adopt an example from the literature (Cánovas et al., 2006). It illustrates that a change in the order of events can have dramatic consequences.

Consider a management strategy that corresponds to target-oriented control (Dattani et al., 2011; Franco and Liz, 2013). The population size is changed by the amount  $H(x) = c(T - x)$ , where  $T$  is the target population size and  $c$  the control effort. That is, the population is harvested if it is beyond the target, and it is restocked otherwise. Strictly speaking, this particular intervention is not an exclusive harvesting method, which is why we interpret it in this section more generally as a control method. Choosing  $T = 1/2$  and



**Fig. 1.** Time series of population dynamics composed of the two processes harvesting ( $H$ ) and reproduction ( $R$ ). Census is taken only after a complete iteration of both processes. The red points give the equilibrium population sizes which are sampled after specific processes, namely after reproduction in (a) and harvesting in (b). Variability in population size within a census time step (blue points) is not measured (but see the framework suggested in Section 6). Obviously, qualitative dynamics are the same, and quantitative differences are only due to the census timing. Note that census after reproduction gives a larger measure of population size than census after harvesting. This is the reason why hydra effects may be observable (a) or hidden (b). (Colour online.)

$c = 2/3$ , the population size after implementing the control becomes

$$h(x) = x + H(x) = \frac{1}{3}(x + 1).$$

Next, assume that the population growth exhibits a strong Allee effect, for which we consider the following caricature model:

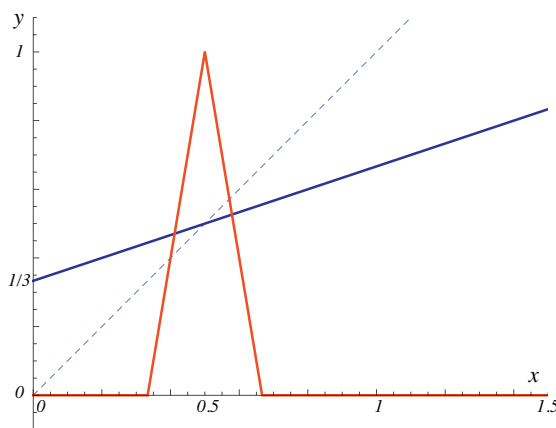
$$f(x) := \begin{cases} 0, & \text{if } x \leq \frac{1}{3} \text{ or } x \geq \frac{2}{3}, \\ 6x - 2, & \text{if } \frac{1}{3} < x \leq \frac{1}{2}, \\ 4 - 6x, & \text{if } \frac{1}{2} < x < \frac{2}{3}. \end{cases}$$

The graphs of  $f$  and  $h$  are shown in Fig. 2.

On the one hand, the composition  $f \circ h$ , which corresponds to ‘census after reproduction’, produces the tent map (when restricted to the interval  $[0, 1]$ ); see Fig. 3a. This map is chaotic (Alligood et al., 1997). Actually, periodic orbits are dense and all of them are unstable, while most solutions fill densely the interval  $[0, 1]$ . From an ecological point of view, this high variability may be undesirable because it bears the risk that perturbations trigger stochastic extinctions (in case of endangered species) or outbreaks (in case of pests), cf. Hilker and Westerhoff (2007).

On the other hand, the map  $h \circ f$ , which corresponds to ‘census after control’, has a positive floor. A large set of initial conditions are driven after one iteration to the fixed point at  $x = 1/3$ , while the behaviour restricted to the interval  $(1/3, 2/3)$  is chaotic. See Fig. 3b.

In this example, the equilibria of  $f \circ h$  are  $K_1 = 0$  and  $K_2 = 2/3$ . The corresponding equilibria of  $h \circ f$  are  $h(K_1) = 1/3$  and  $h(K_2) = 5/9$ . Both  $K_2$  and  $h(K_2)$  are unstable and surrounded by chaotic attractors. Hence, the larger equilibria in each of the models share

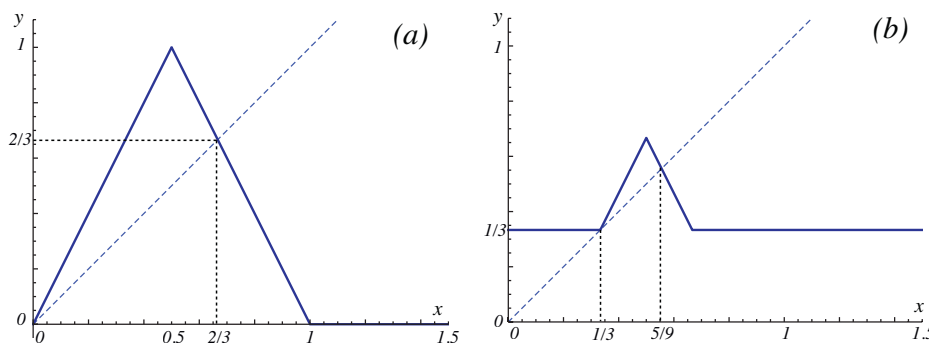


**Fig. 2.** Graphs of the map  $f$  (tent-shaped; red) as a toy model for population reproduction and the map  $h$  (straight line; blue) describing control. The dashed line represents identity. More details in Section 3. (Colour online.)

the same stability. By contrast, there is a significant difference in the stability properties of the smaller equilibria. On the one hand,  $K_1$  is unstable (but it attracts the interval  $[1, \infty)$  in case the population goes extinct). On the other hand,  $h(K_1)$  is semi-stable. It attracts  $h([1, \infty)) = [2/3, \infty)$  and also the interval  $[0, 1/3]$  on the left; notice that  $h \circ f$  is not differentiable at  $h(K_1)$ .

We point out the following difference between the two models:

- If we census the population after control ( $h \circ f$ ), we get the impression that there is a (semi-)stable equilibrium  $h(K_1)$  attracting a large range of initial conditions.



**Fig. 3.** The order of events matters in this example. The graphs show the maps of (a) harvesting before reproduction,  $f \circ h$ ; and (b) harvesting after reproduction,  $h \circ f$ . The maps are defined in Section 3.

- However, if we census the population after reproduction ( $f \circ h$ ), we cannot observe a stable population. Instead, the dynamics are chaotic (with the rare possibility of essential extinction in case the population size becomes  $x = 1$ ; note that we have excluded the interval  $x > 1$  from our considerations).

In short, while the *local* behaviour around the larger equilibria remains the same (i.e., chaotic) independently of census timing, there is a difference in the *global* behaviour. That is, the dynamics change if we start from initial conditions further away from the equilibria. On the one hand, for  $h \circ f$ , the chaotic attractor is the only attractor and it is approached by all orbits starting from any initial condition within the interval considered. On the other hand, for  $f \circ h$ , there are two attracting sets, namely the chaotic one around  $h(K_2)$  and the semi-stable equilibrium  $h(K_1)$ . Which one of these is approached depends on the initial condition. Hence, although the relative order of the two processes is the same, we may get a fundamentally different impression of stability (order versus chaos) and population vulnerability (persistence versus extinction).

The reason that the two compositions  $h \circ f$  and  $f \circ h$  are not topologically conjugated is probably the lack of surjectivity of the target-oriented control method. Biologically, this can be interpreted as follows. Since the control involves restocking depending on the target, this implies that the population cannot fall anymore below a certain range of small population sizes. This is illustrated in Fig. 3 by the map of  $h$  being shifted upwards.

In this section, we have argued that different census timing may lead to different global behaviour. In the forthcoming sections, we show that this is not the case for standard control methods (constant yield harvesting, proportional harvesting and threshold harvesting) with the usual overcompensatory reproduction maps in population dynamics.

#### 4. Constant yield harvesting

Here we demonstrate that the order of events does not matter for the strategy of constant-yield harvesting. We will show that the qualitative dynamics, including global behaviour, are the same independently of census timing. Quantitative effects will be investigated in terms of hydra effects.

As before, consider a discrete-time single-species model

$$x_{n+1} = f(x_n), \tag{4.1}$$

where  $x_n$  denotes the population density in the  $n$ th generation. Function  $f$  is the so-called stock–recruitment relationship, and we assume that the density dependence is overcompensatory. Typical examples are the Ricker map (2.3); the quadratic (logistic) map  $f(x) = rx(1 - x)$  with  $r > 1$ ; and the generalised Beverton–Holt map  $f(x) = rx/(1 + x^\gamma)$ ,  $r > 1$ ,  $\gamma \geq 1$ , all given in scaled form. Schreiber (2001) analysed these three models with a strategy of constant

harvesting after reproduction. A more general model allowing survivorship of adults was treated in Liz (2010a).

Assume that there is a positive constant quota  $d$ , and we census the population stock after a portion  $(1 - \theta)d$  of this quota has been removed ( $\theta \in [0, 1]$ ). In the remainder of this Section, we will take  $\theta$  as a proxy for census timing. We will investigate both the qualitative and quantitative dynamics as a function of  $\theta$ . Note that at one extreme, for  $\theta = 0$ , census takes place after the entire quota has been harvested. This situation has been well-studied for constant-yield harvesting (Sinha and Parthasarathy, 1996; Vandermeer and Yodzis, 1999; Schreiber, 2001; Liz, 2010a). At the other extreme of the spectrum, for  $\theta = 1$ , census takes place after reproduction and before any harvesting occurs. Interestingly, this latter situation has received less attention in the literature.

To get a suitable mathematical setting, we write  $H = \theta H + (1 - \theta)H$ . This reflects that the total amount harvested is made up of a portion removed after census (i.e., before reproduction) and another portion removed before census (i.e., after reproduction). Then the sequence  $RHRHRH\dots$  becomes  $\dots R[(1 - \theta)H] [\theta H]R[(1 - \theta)H] [\theta H]R[(1 - \theta)H] \dots$

The above considerations lead to the following harvesting model:

$$x_{n+1} = [f([x_n - \theta d]_+) - (1 - \theta)d]_+, \tag{4.2}$$

where  $[x]_+ = \max\{x, 0\}$ .

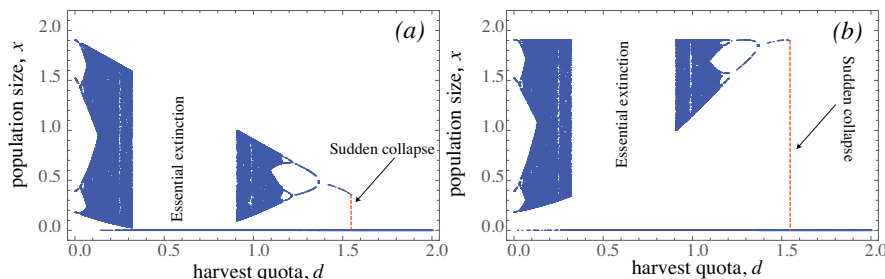
In Appendix A we provide a rigorous analysis of Eq. (4.2) both from a qualitative and a quantitative point of view. In the remainder of this Section, we present the main results.

##### 4.1. Qualitative dynamics

Our first conclusion is that, from the dynamical point of view (which includes such effects as stability, periodicity, chaos and collapses), the value of  $\theta$  is irrelevant. That is to say, a different census timing preserves qualitative behaviour and will not lead to misleading conclusions with respect to the global dynamics of population growth. In particular, sudden collapses, which lead to essential extinction, occur for the same harvesting quotas  $d$  (Fig. 4). The range of values of  $d$  causing essential extinction is exactly the same for all values of  $\theta$ , i.e., independently of the census timing.

##### 4.2. Quantitative dynamics

Having proved that census timing (in form of parameter  $\theta$ ) does not influence the qualitative behaviour of Eq. (4.2), we now direct our attention to the influence of  $\theta$  on quantitative effects. For this, we will focus on hydra effects, for which we measure the mean value of the solutions. To be more precise, we recall some definitions from Sieber and Hilker (2012) (see also Liz and Ruiz-Herrera, 2012). Denote by  $\{x_n(d, \theta)\}_{n \geq 0}$  the solution of Eq. (4.2) for



**Fig. 4.** Qualitative dynamics are not affected by census timing. The panels show bifurcation diagrams of model (4.2) for population census (a) after and (b) before the entire quota has been harvested, i.e.,  $\theta = 0$  and  $\theta = 1$ , respectively. The bifurcation diagrams plot asymptotic population size against harvesting quota. The vertical dashed lines indicate sudden collapses. Reproduction given by  $f(x) = xe^{2.6(1-x)}$ . Note that the diagram for  $\theta = 0$  was first shown by Sinha and Parthasarathy (1996) and Schreiber (2001).

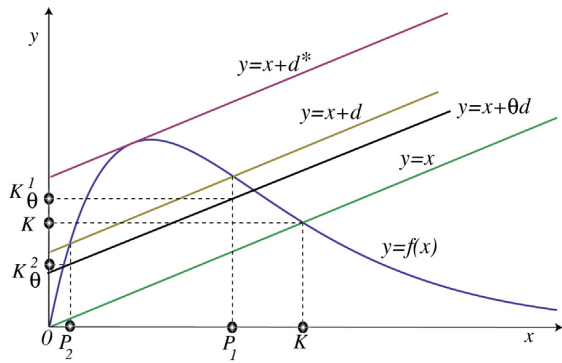


Fig. 5. Geometric interpretation of the positive equilibria of model (4.2).

given parameters  $d \geq 0$  and  $\theta \in [0, 1]$  as well as an initial condition  $x_0 \geq 0$ .

**Definition 4.1.** The mean value map is defined as the function  $\phi : M \times [0, \infty) \times [0, 1] \rightarrow [0, \infty)$  given by

$$\phi(x_0, d, \theta) = \lim_{n \rightarrow \infty} \frac{1}{n} \sum_{i=0}^{n-1} x_i(d, \theta),$$

where  $M \subset [0, \infty)$  is the subset of initial conditions for which the previous limit exists.

**Definition 4.2** (Hydra effect).

For a given value of  $\theta$ , the population governed by Eq. (4.2) experiences a hydra effect if there are an initial condition  $x_0$  and harvesting values  $d_1 < d_2$  such that  $\phi(x_0, d_1, \theta) < \phi(x_0, d_2, \theta)$ . The hydra effect is smooth if  $\phi(x_0, d, \theta)$  is continuous in  $d$  on  $[d_1, d_2]$ , otherwise it is non-smooth.

For each census timing  $\theta$ , the mean value map assigns to an initial condition  $x_0$  and a harvesting quota  $d$  the asymptotic mean value of the solution  $\{x_n(d, \theta)\}_{n \geq 0}$ . For example, if  $K_\theta(d)$  is an equilibrium of Eq. (4.2) then  $\phi(K_\theta(d), d, \theta) = K_\theta(d)$ . We emphasise that  $\phi(x_0, d, \theta)$  provides the mean population size at the moment of its census, that is, after a portion  $(1 - \theta)d$  of the stock has been removed. It is hence clear that the asymptotic mean value of the solutions is an increasing function of  $\theta$ . That is, the mean population size at census increases the more we harvest before reproduction and after census.

An analogous observation applies to the hydra effect. This effect is observed depending on the census timing. Actually, our results in Appendix A show that a hydra effect is observed according to Definition 4.2 if (i) growth rates are high and (ii) at least half of the quota is removed after census (see Proposition A.3).

To have an intuitive idea of why a hydra effect is observed when the equilibrium is stable, it is useful to provide a geometric interpretation of the positive equilibria of (4.2). The condition for  $x$  to be a positive equilibrium is

$$f(x - \theta d) = x + (1 - \theta)d. \quad (4.3)$$

The change of variables  $z = x - \theta d$  transforms (4.3) into  $f(z) = z + d$ . This means that the positive equilibria of (4.2) are obtained in the following way (see Fig. 5).

1 Find the intersection points  $(x, y)$ ,  $x > 0$ , between the line  $y = x + d$  and the curve  $y = f(x)$ . Under conditions (A1)–(A4) in Appendix A, which correspond to overcompensatory population dynamics,

there is only one point  $K$  for  $d = 0$ ; two points  $P_2 < P_1$  for  $0 < d < d^*$ ; one point for  $d = d^*$ ; and no intersection for  $d > d^*$ .  
2 The positive equilibria of (4.2) are obtained as  $K_\theta^1 = P_1 + \theta d$ ,  $K_\theta^2 = P_2 + \theta d$ .

Notice that  $P_i = K_0^i$  for  $i = 1, 2$ .

Since the smaller equilibrium  $K_\theta^2$  is always unstable, we will focus mainly on the response of the larger equilibrium  $K_\theta^1$  to increased harvesting.

Fig. 5 illustrates that the hydra effect is observable when the population census is taken after reproduction, but remains hidden if it is taken after harvesting.

For  $\theta = 0$  (total harvesting before census), we have  $K_\theta^i = P_i$ ,  $i = 1, 2$ , so that  $K_\theta^1$  decreases as the harvesting quota  $d$  is increased (see Fig. 5). At the same time,  $K_\theta^2$  increases until  $K_\theta^1$  and  $K_\theta^2$  collide at  $d = d^*$ , and then they disappear after a tangent bifurcation (Schreiber, 2001). Beyond  $d^*$ , the population is driven to extinction.

Assuming that  $f(K) < 0$ , the behaviour of  $K_\theta^1$  for  $\theta = 1$  (total harvesting after census) is completely different. Population size increases for  $d \in (0, \bar{d})$ ; then decreases until  $K_\theta^1 = K_\theta^2$  at  $d = d^*$ ; and disappears beyond  $d^*$  (see Fig. 5). The value  $\bar{d}$  is obtained as  $\bar{d} = f(c) - c$ , where  $c$  is the point at which  $f$  reaches its maximum value. Notice that  $K_1^1$  and  $P_1$  become stable if the harvest quota exceeds a value  $d^* < \bar{d}$ .

Fig. 6 also suggests that the sudden collapse leading to extinction at  $d = d^*$  is even more dramatic when the population is censused before harvesting, because the population can persist at intermediate sizes and its size reaches the maximum value  $f(c)$  at a stable equilibrium for harvesting quotas slightly smaller than the critical one ( $d = \bar{d}$ ). Notice that there is a signal for caution, but it can be barely appreciated in practical situations: the stable equilibrium starts to decrease when the quota is incremented beyond the value  $\bar{d}$ . Unfortunately, the difference between  $\bar{d}$  and  $d^*$  might be very small.

On the other hand, in the most usual population models governed by (4.1) there is a crisis bifurcation at some critical point

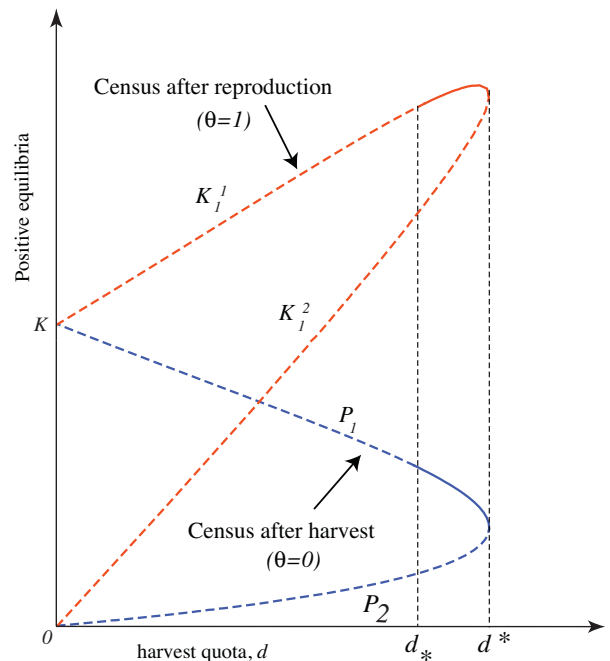


Fig. 6. A hydra effect can be measured for a large range of harvesting quotas (up to  $\bar{d}$ , which is close to  $d^*$ ) for census before harvesting ( $\theta = 1$ ). If the census is taken after harvesting ( $\theta = 0$ ), the hydra effect is hidden and not measured. Solid lines indicate stable equilibria, dashed lines unstable equilibria. Note that the qualitative behaviour does not differ between  $\theta = 0$  and  $\theta = 1$ .



leading from essential extinction to bistability (see e.g., [Vandermeer and Yodzis, 1999](#); [Schreiber, 2001](#); [Liz, 2010a](#)). It is clear that this bifurcation leads to a non-smooth hydra effect, which is observable for all  $\theta \in [0, 1]$ .

**5. More on the hydra effect**

As far as we know, this is the first time that the hydra effect is studied in a exploited population with constant quota harvesting. Actually, the hydra effect seems to be a common feature of single-species discrete-time exploited populations with overcompensatory density dependence, independently of the form of exploitation.

Indeed, if  $x$  is the population size, we denote by  $h(d, x)$  the portion of the population remaining after harvesting with some harvesting strength  $d$ . It is natural to assume that  $h(d, x)$  is a continuous function, increasing in the variable  $x$  and decreasing in the variable  $d$ . For example,  $h(d, x) = \max\{x - d, 0\}$  for constant quota harvesting, where  $d$  denotes the quota; and  $h(d, x) = (1 - d)x$  for proportional harvesting, where  $d$  is the harvesting effort. In the general case, the model with census after reproduction and before harvesting reads

$$x_{n+1} = f(h(d, x_n)). \tag{5.1}$$

The positive equilibria of (5.1) can be found as follows:

1. Find the points  $P$  such that  $h(d, f(P)) = P$ .
2. The points  $f(P)$  are equilibria of (5.1).

Assume that  $f$  is unimodal and has a unique fixed point  $K$  with  $f(K) < 0$ . Since  $h(x) < x$  (the harvest has to be smaller than the population size), the eventual solutions  $P = P(h)$  of  $h(d, f(P)) = P$  close to  $K$  are smaller than  $K$  and decrease with further strength of harvesting. But this fact implies that the points  $K(h) = f(P(h))$  get larger as harvesting pressure increases due to the overcompensatory effect of the density dependence. A consequence is that a hydra effect is observable if the equilibrium becomes asymptotically stable. This is exactly the situation for constant and proportional harvesting.

**5.1. Limiter control**

To illustrate our discussion with another example, consider the limiter control strategy studied in [Hilker and Westerhoff \(2006\)](#). For a more thorough qualitative analysis of this model, see [Sinha \(1994\)](#) and [Stoop and Wagner \(2003\)](#).

If intervention takes place after reproduction and before census, we get the model

$$x_{n+1} = \min\{f(x_n), T\}, \tag{5.2}$$

where  $T$  is the limiter. Note that the smaller is the value of  $T$ , the larger is the intervention. If  $M$  is an upper bound for  $f$ , we call  $d = [M - T]_+$ , in such a way that increasing  $d$  makes the limiter smaller, which means a bigger harvest.

For simplicity, we assume that  $f$  satisfies conditions (A1)–(A3) in [Appendix A](#), and the unique positive equilibrium  $K$  in the absence of harvesting satisfies  $f(K) < 0$ . In this case  $h(d, x) = \min\{x, M - d\} = \min\{x, T\}$ , and the solutions of  $h(d, f(z)) = z$  are

$$z(T) = \begin{cases} K, & \text{if } T \geq K, \\ T, & \text{if } T < K. \end{cases}$$

It is clear that  $z(T)$  is the only positive equilibrium of (5.2) for each value of  $T$ , and  $z(T)$  is a nondecreasing function. This is illustrated in [Fig. 7a](#). Note that a hydra effect is not observable and remains hidden when the population is stable. (If the population is unstable, there may be a hydra effect due to altered population cycles, cf. [Hilker and Westerhoff \(2006\)](#), [Abrams \(2009\)](#).)

On the other hand, if intervention occurs before reproduction and after census we have

$$x_{n+1} = f(\min\{x_n, T\}). \tag{5.3}$$

Positive equilibria of (5.3) are obtained as

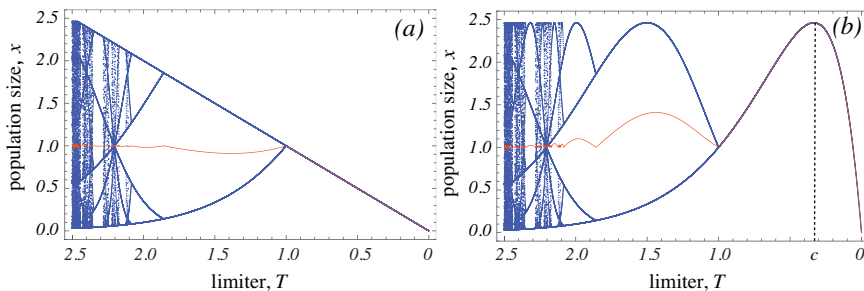
$$K(T) := f(z(T)) = \begin{cases} K, & \text{if } T \geq K, \\ f(T), & \text{if } T < K. \end{cases}$$

This means that when  $T$  ranges from  $K$  to the critical point  $c$ , the equilibrium  $K(T)$  is increasing. Moreover, it is easy to prove that  $K(T)$  is globally attracting, thus making the hydra effect observable. This is illustrated in [Fig. 7b](#), where we can see a hydra effect even for stable populations. That is, the different census timing has revealed the hydra effect.

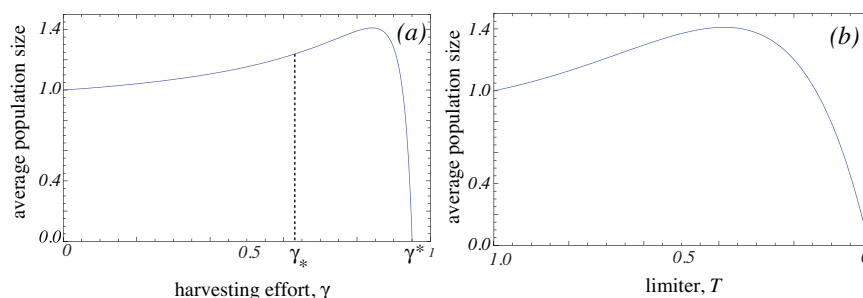
**6. Revealing hidden hydra effects—a more suitable mathematical framework**

As we have shown for the usual overcompensatory population dynamics and harvesting strategies, their temporal ordering does not matter—neither from a qualitative nor from a quantitative point of view. However, if the population is censused only after harvesting, but not after reproduction, the hydra effect may go unnoticed because it is simply not measured. A straight-forward approach to resolve this problem is to census the population after each of the two processes.

Mathematically, this approach can be expressed in the framework of a 2-periodic difference equation (or, more generally, if we consider  $p$  processes,  $p$ -periodic difference equation). For example, the alternation of proportional harvesting (with effort  $\gamma$ )



**Fig. 7.** For the strategy of threshold harvesting, a hydra effect at stable populations (here for limiter values  $T < 1$ ) is (a) hidden for census after harvesting, but (b) observable for census after reproduction. Note the reversed horizontal axis meaning that harvesting strength increases into the right-hand side direction. The red lines give mean values of the solutions. The equilibrium becomes asymptotically stable at  $T = 1$  in both cases. Hydra effects in the unstable range ( $T > 1$ ) are due to a different mechanism, namely that of altered fluctuations. Models in (a) and (b) are given by Eqs. (5.2) and (5.3), respectively, with  $f(x) = xe^{3(1-x)}$ . (Colour online.)



**Fig. 8.** The framework of periodic difference equations can reveal hidden hydra effects. The diagrams show the average population size, given by Eq. (6.2), for two different harvesting strategies: (a) proportional harvesting  $h(x) = (1 - \gamma)x$  with  $\gamma \in [0, 1]$ . The 2-periodic orbit  $\{K, (1 - \gamma)K\}$  is asymptotically stable for  $\gamma \in [\gamma^*, \gamma']$ , where  $\gamma^* = 1 - e^{-1} \approx 0.6321$  and  $\gamma' = 1 - e^{-3} \approx 0.95$ . (b) limiter control  $h(x) = \min\{x, T\}$ , with  $T$  ranging between  $T = 1$  and  $T = 0$ , for which the 2-periodic orbit is globally attracting. In both cases, a hydra effect is still observed. Population dynamics follow the Ricker map  $f(x) = xe^{3(1-x)}$ .

and reproduction (with map  $f$ ) can be described by

$$x_{n+1} = F_n(x_n) := \begin{cases} f(x_n), & \text{if } n \text{ is odd,} \\ (1 - \gamma)x_n, & \text{if } n \text{ is even.} \end{cases} \quad (6.1)$$

In effect, this means that we choose more fine-grained steps  $n$ , which are not necessarily equidistant in physical time anymore. Moreover, the population is measured actually twice, which may come at the expense of additional census effort. However, this framework of periodic difference equations brings to light the various processes that are otherwise implicitly hidden in temporally structured models (see e.g., Åström et al., 1996).

When  $K$  is an attracting positive equilibrium of the composition map  $\pi(x) = f((1 - \gamma)x)$ , then Eq. (6.1) has an attracting 2-periodic orbit  $\{K, (1 - \gamma)K\}$ . A possibility to observe a real hydra effect is checking if the average

$$\frac{K + (1 - \gamma)K}{2} \quad (6.2)$$

may be increasing with harvesting effort  $\gamma$ . We show this effect in Fig. 8 for two different harvesting strategies.

In some sense, this problem has been treated by considering a stage-structured model of juveniles ( $J_n$ ) and adults ( $A_n$ ) with a strategy of adult-only harvest. If  $K$  increases with  $\gamma$ , then there is a hydra effect in the adult population ( $A_n$ ). And if the average increases with  $\gamma$  as well, then there is a hydra effect in the total population ( $J_n + A_n$ ). A hydra effect in  $J_n$  does not occur. See, for example, Zipkin et al. (2009) and Liz and Pilarczyk (2012).

Interestingly, the issue of census time can be considered also in the framework of the Clark model (Clark, 1990, p. 198). He distinguishes between the parent stock,  $P(n)$ , and recruits,  $R(n) = f(P(n))$ , in such a way that a model for constant harvesting  $H$  leads to

$$\begin{aligned} P(n+1) &= R(n) - H = f(P(n)) - H, \\ R(n+1) &= f(P(n+1)) = f(R(n) - H). \end{aligned}$$

Thus, a hydra effect is observed if we census recruits (i.e., after reproduction), but it is hidden if we census the parent stock (i.e., after harvesting).

The framework suggested above seems particularly suitable for another harvesting strategy, namely that of periodic harvesting. For the Neotropical palm species *Euterpe edulis*, for instance, it is recommended that populations in the Brazilian Atlantic Forest recover after harvesting (Reis et al., 2000). This can be modelled by harvesting a population not every other step as in Eq. (6.1), but only every  $k$ th step (cf. Freckleton et al., 2003):

$$x_{n+1} = F_n^k(x_n) := \begin{cases} f(x_n), & \text{if } n \text{ is not a multiple of } k, \\ (1 - \gamma)x_n, & \text{if } n \text{ is a multiple of } k, \end{cases}$$

where we assume proportional harvesting preceding reproduction. This model has been recently analysed by Braverman and Liz (2012); in particular, it has been proved that a globally stable positive equilibrium of the map  $\pi(x) = f((1 - \gamma)x)$  typically leads to a globally attracting  $k$ -periodic solution of the nonautonomous difference equation  $x_{n+1} = F_n^k(x_n)$ .

## 7. Discussion and conclusions

While differential equations are well-suited to model population dynamics with simultaneously occurring processes, difference equations can deal with those processes that take place sequentially (Boyce et al., 1999). In fact, the temporal structure of events has been recognised to be an important determinant of population dynamics (Åström et al., 1996; Jonzén and Lundberg, 1999; Kokko and Lindström, 1998; Kokko, 2001). Somewhat contrary to this realisation, we have shown in this paper that the order of events does not matter if there are two processes only like reproduction and harvesting.

While this has already been suggested by Åström et al. (1996), a simple example illustrates that it is not universally true (cf. Section 3). For the usual population dynamic maps and exploitation strategies, however, we have rigorously proved that there are no qualitative differences in stability properties, and that quantitative differences only arise due to the mere fact of a different time of population census. Actually, the question of one process taking place before or after the other one boils down to the question when the population is sampled. This can have profound consequences as to whether or not phenomena like hydra effects can be observed.

### 7.1. Hidden hydra effects and their implications

When the order of events does not matter qualitatively or quantitatively, this implies that hydra effects occur independently of the temporal structure of processes. In particular, this holds for hydra effects in stable populations (i.e., due to the mechanism of overcompensation and mortality in temporally structured populations). Until now, it was believed that hydra effects in such populations require harvesting to precede reproduction (Kokko, 2001; Seno, 2008; Abrams, 2009). Conversely, harvesting after reproduction would not lead to a hydra effect. For instance, Abrams (2009, p. 467) expressed this as follows: “The lack of a hydra effect in stable discrete generation models with mortality following density dependence is a consequence of the fact that density dependence cannot counteract such mortality”. Seno (2008, p. 65) also concluded that a hydra effect for harvesting after reproduction “never occurs” (highlighting in italics font used by the original author).

**Table 1**  
Population models with harvesting leading to hydra effects.

Control strategy	Reference
Proportional harvesting	Kokko and Lindström (1998), <sup>a</sup> Seno (2008), Abrams (2009), and Liz and Ruiz-Herrera (2012)
Constant harvesting	Kokko (2001) <sup>b</sup>
Threshold harvesting	Hilker and Westerhoff (2006)
Target-oriented control	Dattani et al. (2011) and Franco and Liz (2013)
Proportional harvesting in models with sequential density-dependence	Jonzén and Lundberg (1999)
Proportional harvesting in stage-structured models	Zipkin et al. (2009) and Liz and Pilarczyk (2012)

<sup>a</sup> See their Fig. 3A on p. 299.

<sup>b</sup> See her Fig. 2B on p. 144.

Obviously, hydra effects do take place for harvesting following reproduction as well, but this happens early on within a time step. The increase in population size is obscured by the timing of population census just after harvest. Hence, the actual population increase after reproduction remains 'hidden' even though, taken over the entire time interval and not just at the census time, the population size was greater due to the hydra effect.

Consequently, hydra effects are much more common than previously thought. This may have profound implications for the management of populations. The presence of a hydra effect, even a hidden one, means that managers can achieve two goals simultaneously, namely an increase in the yield as well as in the remaining population size (cf. Kokko, 2001). These two goals typically exclude each other in a Pareto-optimal sense (Bunn, 1984), where an increase in harvest optimises the yield but reduces the remaining population size (or vice versa). If the hydra effect is hidden, managers may miss out on the opportunity to maximise both yield and population size rather than just one of them.

While this appears good news for the sustainable exploitation of renewable resources, hidden hydra effects may prove fatal in other situations. Harvesting often aims at controlling or eradicating pest species. Examples include non-indigenous invasive species or agricultural pests (Hone, 2007). In many cases, harvesting is also established on the damaging effect of unharvested populations (Robinette et al., 1977). Too high population densities of deer, for instance, can lead to overgrazing and an increased number of road accidents (Putman and Moore, 1998). In the presence of hydra effects, however, the control effort can 'backfire' (Zipkin et al., 2009). If the hydra effect is hidden, the resurgence of the pest additionally goes unnoticed as it escapes population census. This may be particularly devastating for the control of invasive species, as their early detection is considered crucial (Simberloff, 2003).

If we interpret harvesting mortality a bit more widely as brought about by predators, hydra effects lend additional support in favour of predator protection programmes. The prey individuals that are removed by an increased predator population are more than compensated for. In fact, the mortality is over-compensatory as additional predation leads to an increased prey population size.

This is related to the concept of a 'doomed surplus', where predation/harvesting removes those individuals that would die anyway (Errington, 1934, 1971). In such a case, one speaks of compensatory mortality as opposed to the case of additive mortality, where harvesting reduces population size. In the case of over-compensatory mortality (hydra effect), the doomed surplus actually turns out to be a burden—the population benefits upon its removal. This is underlined by a reproductive value that is negative rather than positive (Kokko and Lindström, 1998).

The question of when to hunt/harvest and whether harvesting mortality is additive or compensatory, continues to be discussed in the literature (e.g., Pöysä et al., 2004; Milner et al., 2011; Sandercock et al., 2011). The answer for a specific population

probably lies in the details. Nevertheless, the concept of compensatory density-dependence is key for the sustainable harvesting of populations (Nicholson, 1991; Bartmann et al., 1992). The recent insight that harvesting mortality can be over-compensatory (Jonzén and Lundberg, 1999; Kokko, 2001) illustrates the complexity of system behaviour and that we are still in the process of trying to understand the consequences of harvest (Hilborn et al., 1995; Milner-Gulland and Mace, 1998; Struhsaker, 1998; Boyce et al., 1999).

## 7.2. Generality of hydra effects

Hydra effects can occur for any kind of harvesting. This should be obvious by now, but, as far as we know, has never been stated explicitly. In the literature, harvesting strategies of proportional harvesting prevail (Seno, 2008; Abrams, 2009). The essential point, however, is to reduce population size such that the reproductive output increases as a consequence of overcompensatory density-dependence, cf. our mathematical arguments in Section 5. The particular strategy of harvesting is not important, as long as the population is sufficiently reduced.

For unstable populations, there can be another kind of hydra effect. Harvesting (and similarly augmentation) transition the population onto a different cycle, which can have an increased average population size. This kind of hydra effect has been long known to occur also for harvesting following reproduction (Hilker and Westerhoff, 2006; Seno, 2008; Abrams, 2009). An example can be seen in Fig. 7 for limiter control.

Table 1 lists a number of harvesting strategies that have been reported to lead to hydra effects. This collection is not meant to be exhaustive, but to illustrate that population removal per se (rather than its specific way of implementation) is important in triggering hydra effects. Please note that most references in Table 1 do not distinguish between the different types of hydra effect. It is also worth noting that the majority of these papers do not explicitly mention 'hydra effect' as this term has only been recently coined by Abrams (2009).

## 7.3. Uncovering hidden hydra effects and temporal structure

We have proposed the mathematical framework of periodic difference equations to 'elucidate' hidden hydra effects. In some sense, this approach corresponds to the suggestion that "one has to sample the population at least as many times a year as there are sequential density-dependent processes [...]" (Åström et al., 1996, p. 180). However, there can be biological constraints when measurements are possible. Lutscher and Petrovskii (2008) discuss a few of such examples. For instance, it might be impossible to census juveniles of a certain species. Hence, in such cases, there might be hydra effect, but it could not be observed.

It has been argued before (Kokko and Lindström, 1998) that the mere relationship between two census time points does not always suffice to reflect the actual response of populations to



perturbations. The approach suggested in this paper releases the system from the choice of census timing.

On the downside, more census data require increased sampling effort. From a practical point of view, this may be costly or impossible (e.g., due to expensive labour, remote locations or extreme seasons).

On the upside, if there is refined census data available, we could think about using not only their plain averages, but to give population sizes different weights at different points in time. This could reflect the time length of certain processes or attribute priorities to some events from a management point of view.

Periodic difference equations have been used to model the effect of seasonality on population growth (Kot and Schaffer, 1984). In order to assess whether seasonal fluctuations are deleterious or advantageous for the population, the average of 2-periodic difference equations has been studied intensively (Costantino et al., 1998; Henson and Cushing, 1997; Cushing and Henson, 2001; Kon, 2005; Elaydi and Sacker, 2006). More recent papers studying periodic difference equations in the context of population dynamics are by Elaydi et al. (2011) and Pötzsche (2013). A similar framework has been used to investigate Parrondo's paradox (Peacock-López, 2011).

#### 7.4. Mathematical results

It has been argued before that the temporal structure of events does not matter if their relative order is the same (Åström et al., 1996). This is convincing when harvesting is described mathematically by a bijective function (for example,  $h(x) = (1 - \gamma)x$  for proportional harvesting). If the map  $h$  is not an homeomorphism, however, then it is not so clear (from a mathematical point of view) that the dynamics of  $f(h(x))$  and  $h(f(x))$  are the same.

An example where this is not the case is given in Section 3. The dynamics of  $f(h(x))$  and  $h(f(x))$  are still equivalent regarding periodic points and their stability—but there are 'global differences' due to the lack of surjectivity of the composition. What are the practical consequences of these global differences? While populations starting close to the equilibrium share its dynamical behaviour, orbits starting further away may be attracted to a different dynamical regime. This may affect aspects such as essential extinction, which is basically a global phenomenon (Sinha and Parthasarathy, 1996; Schreiber, 2001; Liz, 2010a).

Admittedly, examples like the one in Section 3 are somewhat pathologic, but actually not too unrealistic. The modified tent map is a commonly employed toy model for population dynamics with strong Allee effect. The target of 1/2 in the harvesting strategy is close to the population's carrying capacity (cf. Fig. 2) and may reflect a typical situation in practice (Dattani et al., 2011). The control effort of  $c = 2/3$ , however, could be considered quite high.

Nevertheless, the example reveals potential pitfalls. As for qualitative effects, one census time could give us the impression that the dynamics is, for example, chaotic, while sampling at a different time we could think that the population is essentially stabilised. Of course, this difference only appears if the compositions  $f(h(x))$  and  $h(f(x))$  display different dynamics (as in the example of Cánovas et al., 2006). Regarding quantitative effects, we discuss these differences in the framework of the hydra effect (placing special emphasis on possibly misleading conclusions derived from sampling the population only once). Thus, it makes sense to investigate this problem for the usual harvesting strategies.

If we restrict our attention to hydra effects for stable populations, then it is easy to argue why proportional harvesting, constant yield harvesting and threshold harvesting preserve stability of the equilibria independently of the order of events.

For proportional feedback, since  $h$  is a homeomorphism, both compositions are topologically conjugated, and hence they share the same dynamics (different observation times only lead to quantitative differences). For constant yield harvesting, this property is not mathematically evident because  $h$  is not one-to-one, so we provide some rigorous results. It may be worth noting that constant yield harvesting is not injective when the population becomes extinct. Hence, it makes sense that the qualitative features are the same. The only not so smooth case is threshold harvesting, which is neither one-to-one nor surjective.

Actually, all these methods preserve stability in the sense that if  $K$  is a stable smooth equilibrium of  $f(h(x))$  with sink of attraction  $(a, b)$  then  $h(K)$  is a stable equilibrium of  $h(f(x))$ , and its sink of attraction contains  $h((a, b))$ .

#### 7.5. Limitations and prospects

In this paper, we have restricted ourselves to simple models with two processes only, namely reproduction and harvesting. That the order of two events does not matter has been recognised before, e.g., for reproduction and predation (Åström et al., 1996, after Crawley, 1992).

Real situations, however, can be more complex. Reproduction could be split into separate birth and death processes (see Jonzén and Lundberg, 1999), or we could consider additional processes, seasonal variations or dynamics taking place in different habitats (which seems relevant for migratory species like waterfowl). Future work could consider models where the temporal order of these processes actually matters, i.e., when there are more than two processes.

Furthermore, some of the processes may not be instantaneous (e.g., natural mortality or continuous harvesting). Kokko and Lindström (1998) investigated the timing of harvesting in this context. Their model allows for continuous harvesting throughout certain hunting seasons. This spurred discussion of not only the order of events, but also of their duration and the case when density-dependence is not instantaneous (reviewed in Ratikainen et al., 2008).

Note that there is some similarity to periodic matrix models. Cyclic permutations give the same population growth rate (i.e., dominant eigenvalue), but may produce different yields (Double-day, 1975). This roughly corresponds to the situation where the order of events does not matter and quantitative differences are due to census timing. Non-cyclic permutations, by contrast, do not preserve the population growth rate (Caswell, 2001; Mertens et al., 2006). Some of the harvesting and control methods considered here assume that the amount of the population removed (or added) depends on the current population size (e.g., proportional feedback or target-oriented control). This implies that the population can be censused for the intervention or that the intervention takes place with a constant effort and is proportional to the population size. Note that there are some conditional harvesting strategies, however, where interventions occur only if a certain threshold is passed. Costa and Faria (2011) and Franco and Perán (2013) consider such threshold harvesting strategies, but obtain different results even though they consider reproduction and harvesting only. The reason is that the conditional harvesting imposes a threshold, which effectively implements a third process (cf. Franco and Perán, 2013).

Our results concern populations at a stable equilibrium. This means that we deal with hydra effect that arise from the temporal separation of mortality and density dependence (Abrams, 2009). A different question is when the population cycles. In this case, the average of a, say, 2-periodic attractor for the harvesting model can increase even if we assume harvesting occurs after reproduction

(and we measure the population after harvesting). Little has been done analytically for this type of hydra effects.

**Acknowledgements**

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**Appendix A**

Here we analyse the model for constant yield harvesting (4.2) from the main text.

We list the main assumptions on the reproduction map, following Schreiber (2001).

- (A1)  $f: [0, \infty) \rightarrow [0, \infty)$  is continuous,  $f(0) = 0$ ,  $f(x) > 0$  for all  $x \in (0, L)$ , and  $f(x) = 0$  for all  $x \geq L$ , where  $0 < L \leq \infty$ .
- (A2)  $f$  has only two nonnegative fixed points  $x = 0$  and  $x = K > 0$ ,  $f(x) > x$  for  $0 < x < K$ , and  $f(x) < x$  for  $x > K$ .
- (A3)  $f$  restricted to  $(0, L)$  is twice differentiable and has a unique critical point  $c < K$  in such a way that  $f'(x) > 0$  for all  $x \in (0, c)$ ,  $f'(x) < 0$  for all  $x > c$ , and  $f''(x) < 0$  on  $(0, c)$ .
- (A4)  $f$  restricted to  $(0, L)$  is three times differentiable, and  $(Sf)(x) < 0$  for all  $x \in (0, c) \cup (c, L)$ , where

$$(Sf)(x) = \frac{f'''(x)}{f'(x)} - \frac{3}{2} \left( \frac{f''(x)}{f'(x)} \right)^2$$

is the Schwarzian derivative of  $f$ .

We emphasise that many usual population models meet assumptions (A1)–(A4) (see e.g., Schreiber, 2001; Liz, 2010b).

**A.1. Qualitative effects of harvesting**

For simplicity, we denote

$$h_\theta(x) = [x - \theta d]_+ = \max\{x - \theta d, 0\},$$

so Eq. (4.2) can be rewritten as

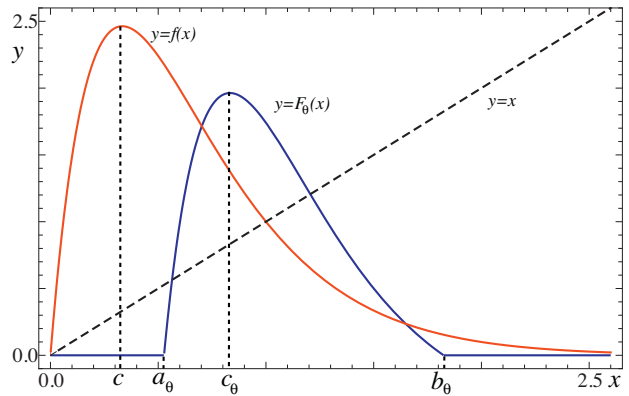
$$x_{n+1} = h_{1-\theta}(f(h_\theta(x_n))) := F_\theta(x_n). \tag{A.1}$$

Since  $h_0(x) = x$ , for all  $x \geq 0$ , in the cases  $\theta = 0$  and  $\theta = 1$  we have, respectively,  $F_0(x) = h_1(f(x))$ ,  $F_1(x) = f(h_1(x))$ , where  $h_1(x) = \max\{x - d, 0\}$ .

Since  $f(c)$  is the maximum value of  $f$ , it is clear that if  $f(c) \leq (1 - \theta)d$  then  $F_\theta(x) = 0$  for all  $x \geq 0$ . Otherwise functions  $F_\theta$  satisfy the following property (see Fig. A.9).

**Proposition A.1.** Assume that  $f$  satisfies (A1)–(A4), and  $f(c) > (1 - \theta)d$ . Then there is an interval  $[a_\theta, b_\theta] \subset (\theta d, L + \theta d)$  such that  $F_\theta(x) > 0$  if and only if  $x \in (a_\theta, b_\theta)$ . Moreover,  $F_\theta$  has a unique critical point  $c_\theta = c + \theta d \in (a_\theta, b_\theta)$  and at most two positive fixed points for all  $\theta \in [0, 1]$ .

**Proof.** Since  $f(h_\theta(c + \theta d)) = f(c) > (1 - \theta)d$ , we have  $F_\theta(c_\theta) = f(c) - (1 - \theta)d > 0$  and  $F'_\theta(c_\theta) = f'(c) = 0$ . By continuity, there are two points  $a_\theta, b_\theta$  such that  $0 < a_\theta < c_\theta < b_\theta < L$ , and



**Fig. A.9.** Graphs of the maps  $f(x)$  and  $F_\theta(x)$ , with  $f(x) = xe^{3(1-x)}$ ,  $d = 1$ ,  $\theta = 0.5$ . The positive fixed points of  $F_\theta$  are determined by the intersections of the line  $y = x$  and the graph of  $F_\theta$ .

$F_\theta(x) > 0$  if and only if  $x \in (a_\theta, b_\theta)$ . By (A3),  $F'_\theta(x) > 0$  on  $(a_\theta, c_\theta)$ , and  $F'_\theta(x) < 0$  on  $(c_\theta, b_\theta)$ . Thus,  $c_\theta$  is the only critical point of  $F_\theta$ .

Since  $F_\theta$  is decreasing on  $(c_\theta, b_\theta)$ , it is clear that  $F_\theta$  cannot have more than one fixed point in that interval. On the other hand, since  $F''_\theta(x) < 0$  on  $(a_\theta, c_\theta)$ , there are at most two fixed points on  $(a_\theta, c_\theta)$ . If there are two fixed points  $K_\theta^1 > K_\theta^2$  in that interval, then  $F'_\theta(K_\theta^1) < 1$  and  $F'_\theta(K_\theta^2) < 1$  for all  $x \in (K_\theta^1, c_\theta)$ . This means that  $F_\theta(x) < x$  for all  $x > K_\theta^1$ , and therefore  $K_\theta^1, K_\theta^2$  are the only positive fixed points of  $F_\theta$ .  $\square$

It is clear from this proposition that if  $f$  satisfies (A1)–(A4) then  $F_\theta$  meets assumptions (A1)–(A5) in Schreiber (2001, Theorem 1). This means that the dynamics of (4.2) falls in one of the following three categories:

- **Extinction:** The unique fixed point is  $x = 0$ , and it attracts all solutions of (4.2).
- **Essential extinction:** Not all solutions of (4.2) converge to zero, but a randomly chosen initial density leads to extinction with probability one.
- **Bistability:** There are two attractors:  $\mathcal{A}_1 = \{0\}$  and  $\mathcal{A}_2$ . The basin of attraction of  $\mathcal{A}_2$  is bounded away from zero and it contains the initial values of the population for which it persists indefinitely.

**Remark A.1.** There are three possibilities for the fixed points of  $F_\theta$ :

1. The map  $F_\theta$  has no positive fixed points if  $F_\theta(x) < x$  for all  $x > 0$ .
2. The map  $F_\theta$  has exactly one positive fixed point  $K_\theta^1$  if  $F_\theta(x) < x$  for all  $x > 0$ , except for  $K_\theta^1$ .
3. The map  $F_\theta$  has exactly two positive fixed points otherwise. In this case, we denote them by  $K_\theta^1 > K_\theta^2 > 0$ .

A key property is that the only factors that determine the category for each particular map  $F_\theta$  are the number of fixed points of  $F_\theta$  and the signs of  $F_\theta(c_\theta) - c_\theta$  and  $F_\theta^2(c_\theta) - F_\theta^3(c_\theta)$ , where  $c_\theta$  is the critical point of  $F_\theta$  and  $F_\theta^k$  represents  $k$  iterations of  $F_\theta$ , that is,

$$F_\theta^k = \underbrace{F_\theta \circ \dots \circ F_\theta}_k.$$

To be more precise, we state the following consequence of Lemma 1 and Theorem 1 in Schreiber (2001). Following the notation in

Schreiber (2001), we denote  $K_\theta^* = F_\theta^{-1}(p)$ , where  $p$  is the smallest positive equilibrium of  $F_\theta$ .

**Proposition A.2.** Assume that  $f$  satisfies (A1)–(A4). Then:

1. (Extinction) If  $F_\theta(x) < x$  for all  $x > 0$  then  $\lim_{n \rightarrow \infty} F_\theta^n(x) = 0$ , for all  $x \geq 0$ .
2. (Bistability)
  - (a) If  $F_\theta(x) \geq x$  for some  $x > 0$ , and  $F_\theta(c_\theta) \leq c_\theta$  then  $K_\theta^1$  is attracting. The basin of attraction of  $K_\theta^1$  is the interval  $J_\theta = (K_\theta^2, K_\theta^*)$ , if there are two positive equilibria, or  $[K_\theta^1, K_\theta^*]$  if there is exactly one positive equilibrium. In both cases, the set  $[0, \infty) \setminus [p, K_\theta^*]$  is attracted by 0.
  - (b) If  $F_\theta(c_\theta) > c_\theta$  and  $F_\theta^2(c_\theta) < F_\theta^3(c_\theta)$ , then  $F_\theta$  has two positive fixed points. The interval  $I_\theta = [F_\theta^2(c_\theta), F_\theta(c_\theta)]$  is invariant, attracting, and contains  $K_\theta^1$ . The basin of attraction of  $I_\theta$  is  $J_\theta$ , and 0 attracts the set  $[0, \infty) \setminus [K_\theta^2, K_\theta^*]$ .
3. (Essential extinction) If  $F_\theta(c_\theta) > c_\theta$  and  $F_\theta^2(c_\theta) > F_\theta^3(c_\theta)$ , then the solution of (4.2) corresponding to a randomly chosen initial condition converge to zero with probability one.

Based on Proposition A.2, we aim to show that, for every fixed value of  $d$ , the dynamical behaviour of  $F_\theta$  and  $F_0$  is equivalent for all  $\theta \in (0, 1]$ .

**Theorem A.1.** Assume that  $f$  satisfies (A1)–(A4). If for a fixed value of  $d \geq 0$  one of the situations described in Proposition A.2 holds for  $F_0$ , then the same situation holds for  $F_\theta$ , for every  $\theta \in (0, 1]$ . In case of bistability, if  $I_\theta$  and  $J_\theta$  are the intervals defined in Proposition A.2, the following relations hold:  $I_\theta = I_0 + \theta d$ , and  $J_\theta = J_0 + \theta d$ , for all  $\theta \in (0, 1]$ . Moreover, if  $\{x_n\}_{n \geq 0}$  is an orbit of  $F_0$  starting at a point  $x_0 \in J_0$ , then the orbit of  $F_\theta$  starting at  $x_0 + d\theta \in J_\theta$  is  $\{x_n + d\theta\}_{n \geq 0}$ . In particular, the dynamics of  $F_\theta$  and  $F_0$  on the corresponding nontrivial attractors are the same for all  $\theta \in (0, 1]$ .

**Proof.** We need some auxiliary results. Their proofs are elementary and thus we only include some of them.

**Lemma A.1.** For all  $\theta \in [0, 1]$  and all  $x \geq 0$ ,  $h_\theta(h_{1-\theta}(x)) = h_1(x)$ .

**Lemma A.2.** Let  $c_\theta = c + \theta d$  be the critical point of  $F_\theta$ . Then,  $h_\theta(c_\theta) = c$ , for all  $\theta \in [0, 1]$ .

**Lemma A.3.** The inequality  $F_\theta(x) < x$  holds for all  $x > \theta d$  if and only if  $F_0(x) < x$  is true for all  $x > 0$  (notice that  $F_\theta \equiv 0$  on  $[0, \theta d]$ ).

**Lemma A.4.** For all  $\theta \in [0, 1]$  and all  $x \geq 0$ ,  $h_\theta(F_\theta(x)) = F_0(h_\theta(x))$ .

**Lemma A.5.** For all  $\theta \in [0, 1]$ , and all integer  $n \geq 1$ ,  $h_\theta(F_\theta^n(c_\theta)) = F_0^n(c)$ .

**Proof.** For  $n = 1$ , we have, by Lemmas A.2 and A.4,

$$h_\theta(F_\theta(c_\theta)) = F_0(h_\theta(c_\theta)) = F_0(c).$$

For  $n = 2$ , we get, by Lemma A.1,

$$\begin{aligned} h_\theta(F_\theta^2(c_\theta)) &= (h_\theta \circ h_{1-\theta} \circ f \circ h_\theta \circ h_{1-\theta} \circ f \circ h_\theta)(c_\theta) = (h_1 \circ f \circ h_1 \circ f)(c) \\ &= F_0^2(c). \end{aligned}$$

Using the same arguments, we arrive at

$$h_\theta(F_\theta^n(c_\theta)) = (h_1 \circ f)^n(h_\theta(c_\theta)) = F_0^n(c).$$

for every  $n \geq 2$ .  $\square$

**Lemma A.6.** For all  $\theta \in [0, 1]$ ,  $F_\theta(c_\theta) > c_\theta$  if and only if  $F_0(c) > c$ .

**Proof.** Since  $c_\theta = c + \theta d > \theta d$ , we have, by Lemma A.5,

$$F_\theta(c_\theta) > c_\theta \Leftrightarrow h_\theta(F_\theta(c_\theta)) > h_\theta(c_\theta) \Leftrightarrow F_0(c) > h_\theta(c_\theta) = c.$$

$\square$

**Lemma A.7.** For each  $\theta \in [0, 1]$ , let  $I_\theta = [F_\theta^2(c_\theta), F_\theta(c_\theta)]$ . Then  $h_\theta(I_\theta) = I_0$ .

**Proof.** It is a straightforward consequence of Lemma A.5.  $\square$

**Lemma A.8.** For all  $\theta \in [0, 1]$ ,  $F_\theta^2(c_\theta) < F_\theta^3(c_\theta)$  if and only if  $F_0^2(c) < F_0^3(c)$ .

**Proof.** By Lemma A.5, it is clear that  $F_\theta^2(c_\theta) > 0$  if and only if  $F_0^2(c) > \theta d$ . Thus, using Lemma A.5 again, it follows that

$$F_\theta^2(c_\theta) < F_\theta^3(c_\theta) \Leftrightarrow h_\theta(F_\theta^2(c_\theta)) < h_\theta(F_\theta^3(c_\theta)) \Leftrightarrow F_0^2(c) < F_0^3(c).$$

$\square$

Now we can prove Theorem A.1. Lemmas A.3, A.6 and A.8 imply that the classes of dynamics from Proposition A.2 occur for the same values of the parameter  $d$ , regardless of the value of  $\theta \in [0, 1]$ .

Lemmas A.4 and A.7 imply that the restrictions of  $F_\theta$  and  $F_0$  to  $I_\theta$  and  $I_0$ , respectively, are topologically conjugated (see e.g., Alligood et al., 1997). In particular,  $h_\theta$  maps orbits of  $F_\theta$  into orbits of  $F_0$ .

The relationship  $I_\theta = I_0 + \theta d$  follows from Lemma A.7, so it only remains to prove that  $J_\theta = J_0 + \theta d$ . Since we already know that  $K_\theta^2 = K_0^2 + \theta d$ , we have to prove that  $K_\theta^* = K_0^* + \theta d$ . Indeed, since  $F_\theta(K_0^* + d\theta) = h_{1-\theta}(f(K_0^*))$ , we get:

$$\begin{aligned} h_\theta(F_\theta(K_0^* + d\theta)) &= h_1(f(K_0^*)) = F_0(K_0^*) = K_0^2 \Rightarrow F_\theta(K_0^* + d\theta) \\ &= K_0^2 + d\theta = K_\theta^2. \end{aligned}$$

Hence, by the definition of  $K_\theta^*$ , it follows that  $K_\theta^* = K_0^* + \theta d$ .  $\square$

A consequence of Theorem A.1 is that the length of the interval  $I_\theta$  does not depend on  $\theta$  (but it is shifted up as  $\theta$  is increased from  $\theta = 0$  to  $\theta = 1$ ). This gives the main result that the qualitative dynamics are the same independently of the census timing.

## A.2. Quantitative effects of harvesting

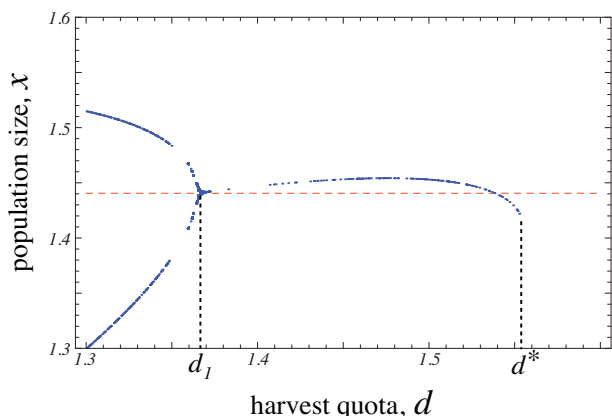
It is not difficult to prove that the population governed by Eq. (4.2) experiences a hydra effect in the case  $\theta = 1$ . Actually, the following result holds:

**Proposition A.3.** If (A1)–(A4) hold and  $f'(K) < -1$ , then the population governed by (4.2) experiences a smooth hydra effect for all  $\theta \in (1/2, 1]$ . If  $-1 \leq f'(K) < 0$  and  $f''(K) < 0$ , then there is a hydra effect if  $\theta \in (1/(1 - f'(K)), 1]$ .

**Proof.** Denote by  $K_\theta^1$  the largest fixed point of  $F_\theta$ . The point  $x = K_\theta^1$  satisfies the equation

$$f(x - \theta d) - (1 - \theta)d - x = 0.$$

If  $-1 \leq f'(K) < 0$ , then the positive equilibrium  $K$  of  $f$  is asymptotically stable. Moreover, since  $f''(K) < 0$ , it follows from



**Fig. A.10.** Magnification of the bifurcation diagram of model (4.2) with constant yield harvesting. A smooth hydra effect occurs on an interval  $(d_1, d_1 + \varepsilon)$  for some  $\varepsilon > 0$ . The dashed line corresponds to the positive equilibrium  $K_\theta^1$  at the point  $d_1 = 1.36423$ , at which there is a period-halving bifurcation leading to an asymptotically stable equilibrium. A collapse leading the system to extinction occurs at  $d^* = 1.5549$ . Parameter values:  $\theta = 0.7$  and  $f(x) = xe^{2.6(1-x)}$ .

(A3) and (A4) that  $f'(x) < 0$  on  $(0, K)$ . Hence,  $F'_\theta(K_\theta^1) = f'(K_\theta^1 - \theta d) = f'(K_\theta^1) \geq f'(K)$ , because  $K_0^1 = P_1 < K$ . Therefore,  $K_\theta^1$  is asymptotically stable, too. Since for an initial condition  $\xi$  in the basin of attraction of  $K_\theta^1$  the mean value  $\phi(\xi, d, \theta)$  is  $K_\theta^1$ , it is enough to prove that  $\partial K_\theta^1 / \partial d > 0$  at  $d = 0$ . At  $d = 0$ , we get, using implicit differentiation,

$$\frac{\partial K_\theta^1}{\partial d} = \frac{\theta f'(K) + 1 - \theta}{f'(K) - 1} > 0 \Leftrightarrow \theta > \theta_0 = \frac{1}{1 - f'(K)}.$$

Next we consider the case when  $f'(K) < -1$ . It is easy to prove that there is a harvesting quota  $d_1 > 0$  for which the equilibrium  $K_\theta^1$  of  $F_\theta$  satisfies  $F'_\theta(K_\theta^1) = -1$ , and  $K_\theta^1$  is asymptotically stable for all  $d \in [d_1, d^*]$ . Using implicit differentiation as before, we get that, at  $d = d_1$ ,

$$\frac{\partial K_\theta^1}{\partial d} = \frac{\theta f'(K_\theta - d_1\theta) + 1 - \theta}{f'(K_\theta - d_1\theta) - 1} = \frac{-1 + 2\theta}{2} > 0 \Leftrightarrow \theta > \frac{1}{2}.$$

□

Proposition A.3 states that in many cases constant yield harvesting leads to an observable hydra effect when at least half of the quota is removed before reproduction (and after population census). This is illustrated for  $\theta = 0.7$  in Fig. A.10, where the bifurcation diagram shows a hydra effect occurring at  $d = d_1$ . Fig. A.10 also displays a crisis bifurcation leading to essential extinction at  $d = d^*$ .

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